Neth. J. Pl. Path. 92 (1986) 115-125

Relative humidity and wind velocity associated with diurnal rhythmicity of aerial dispersal of *Puccinia arachidis* urediniospores

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Accepted 7 November 1985

Abstract

Four groundnut plots were inoculated with *Puccinia arachidis* during the growing season 1984 in Adiopodoumé (Ivory Coast). Rust intensity assessments and spore trappings were performed during the development of the resulting epidemics. Spore density in the air at canopy height ranged from 0 to 800 spores m^{-3}. A significant linear regression was found of the logit of the relative air spore content on the logit of rust intensity expressed as the number of lesions m^{-2} of field. During the first sporulation wave following inoculation, the spore density in the air and the spore content of the pustules were determined at regular intervals. These data were related to weather parameters measured simultaneously. The spore content of the air ranged from 0 to 20 spores m^{-3}. A pronounced daily rhythmicity was found in the spore density of the air, related to a daily rhythm in the depletion and repletion of uredinia. The major explanatory variable was relative humidity, a secondary was wind velocity. The hypothesis is made that this periodicity affects the whole range of variation of aerial spore densities measured at different rust intensities.

Additional keywords: epidemiology, groundnut, rust, weather

Introduction

Many fungal diseases, especially those affecting the aerial parts of plants, depend on air-borne dispersal. As rust *(Puccinia arachidis)* is a major yield-reducing factor of groundnut in Ivory Coast, some aspects of its aerial dispersal were studied.

The aeromycology of groundnut rust was studied by Mallaiah and Rao (1982) in India. These authors observed that the density of urediniospores, usually ranging from 0 to 350 spores m^{-3}, followed a daily periodicity with a maximum when relative humidity was near to 70-80%. They did not supply specific information on disease intensity, but suggested a strong correlation between disease intensity and spore content of the air. Further knowledge on the relations between the spore content of the air and disease intensity as well as weather factors, the objectives of the present study, should provide a better understanding of groundnut rust epidemics.

Materials and methods

The results of two analyses are reported. In the first, spores were trapped in four groundnut plots previously inoculated with rust in order to study the spore content of the air at variable disease levels. The second refers to a series of air samplings which were performed simultaneously with regular measurements of weather parameters in one plot.

Experimental plots and inoculations. Four square (10 m × 10 m) plots were sown on 13 June (plot 1), 2 July (plot 2), 17 July (plot 3) and 1 August (plot 4), 1984, with a local, erect, shortcycle cultivar, highly susceptible to rust, at a rate of 167 000 plants ha^{-1}. Field inoculations were performed to enhance natural rust epidemics.

Plot 1 was inoculated with rust urediniospores on the eveningof 23 July by spraying each of 10 plants in the center of the plot with 10 ml of a suspension containing 30 000 spores ml^{-1} in tap water with 0.005 % (v/v) Triton X-100. This inoculum was supplied by inoculated leaflets under laboratory conditions (Savary, 1985). After inoculation, the plants were covered with plastic bags which were removed early in the next morning.

The centers of the other plots (2,3 and 4) were inoculated on 5 September by dusting dry urediniospores mixed with kaolin onto the plants. In order to obtain equivalent inoculum densities per unit of leaf area with the same amounts of spores, estimates of the number of green leaves per plant were made in the plots before inoculation. In accordance with these estimates, 7, 9 and 10 plants were inoculated in plots 2, 3 and 4, respectively. An amount of 1800 mg of a mixture containing approximately 500 spores mg^{-1} (i.e. approximately 9×10^5 spores per plot, instead of 3×10^6 suspended spores for plot 1) was employed for each plot.

Spore content of the air. Single rotating impaction (Rotorod) samplers were placed in the middle of each plot, among inoculated plants, at canopy top level (approximately 25 cm height). In plot 1, the air was sampled ten times a day from 5.00 a.m. to 7.00 p.m. during four consecutive days, from 6 August to 10 August. In the other plots (2, 3 and 4), spores were trapped at least twice a week, usually at 10 a.m. The sampling duration was 30 minutes at all times. Spore densities in the air (expressed in spores m^{-3}) were calculated from spore counts on the exposed rods, according to the manufacturer's specifications.

Rust intensity. Disease intensity was assessed at least weekly. The disease rating system involved severity ratings of three leaf layers (the 3rd, 5th and last layer from the top along the main stem) on each of the inoculated plant. The mean severity of leaflets (in percent of the leaf area visibly affected by rust) was multiplied by the proportion of diseased leaves to obtain the final rust severity value. To estimate the number of lesions per square meter of field, the individual leaflet ratings were replaced by the mean number of uredinia corresponding to their severity class, and the mean number of lesions per plant was calculated.

Analysis of results. The comparison between the spore content of the air and the disease levels follows Burleigh et al. (1969). Uredial numbers and spore densities were

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Titre original Relative humidity and wind velocity associated with diurnal rhythmicity of aerial dispersal of Puccinia arachidis urediniospores
Netherlands Journal of Plant Pathology 92:115-125 (1986)

Titre en Anglais Relative humidity and wind velocity associated with diurnal rhythmicity of aerial dispersal of Puccinia arachidis urediniospores

Titre en Français Association de l'humidité et de la vitesse du vent avec le rythme quotidien de dissémination des spores de Puccinia arachidis

Mots clés matières épidémiologie, rouille de l'arachide, microclimat, microclimatologie, régressions, piégeage de spores

Résumé en Français Des infections artificielles ont été établies au champ, afin d'étudier les relations entre microclimat et dissémination des spores. Le rythme quotidien de dispersion de spores est en premier lieu associé aux variations d'humidité relative, et en second lieu, aux variations de la vitesse du vent.

Résumé en Anglais (voir article)

transformed into logits,

$$\text{Log}_e \frac{x}{1-x} = \text{Log}_e \frac{N/K}{(K-N)/K},$$

where N represents the current density of spores in the air, K = 1000 spores m^{-3}, the highest density measured in Ivory Coast. When N represents the current density of uredinia in the crop (infected center) with a leaf area index 4, K = 679 000 uredinia m^{-2}. The relation between uredinia m^{-2} and spores m^{-3} was studied by linear regression analysis.

Spore content of the lesions (plot 1). Five leaflets were taken at random at 5.00 a.m., 12.00 a.m. and 7.00 p.m. from the inoculated plants of plot 1. In these samples, the numbers of open and not-yet-open pustules were counted. The leaflets were cut into pieces and shaken in water with 0.01% (v/v) Triton X-100 during 30 minutes. The spore density of each of the resulting five suspensions (one per leaflet) was determined by means of a haemocytometer, and the mean number of spores per open pustule was calculated.

Weather data (plot 1). In plot 1, horizontal wind speed was measured by a rotating cup anemometer placed in the plot at 25 cm above ground, the height of the canopy top. Temperature and relative humidity were registered by a portable thermohygrograph at the edge of the plot, protected from direct insolation by a palm leaf shelter (approx. 1 m^2). The proportion of wet leaves was estimated by direct observation of the 3rd, 5th and last leaves (from the apex) of 5 plants. The measurements were performed simultaneously with the air samplings; they began on 6 August and were performed 10 times a day from 5.00 a.m. to 7.00 p.m.

Results

Inoculations. Rust intensity was lowest in plot 1 (Fig. 1), probably as a result of the inoculation technique employed in this plot, viz. inoculation with a spore suspension. If so, the result is a confirmation of previous comparisons of inoculation methods under laboratory conditions (Savary, 1985). On 5 August, rust severity of the inoculated plants in plot 1 was 3.5% (10 plants) against 1.0% outside the inoculated area (40 plants). Light natural infection contributed to moderate the difference between inoculated and non-inoculated plants, but a Student's t test for small samples shows its significance at $P < 0.01$ ($t = 6.3$).

Rust severity and spore content of the air (plots 1, 2, 3 and 4). To relate spore density of the air to rust intensity of the crop (inoculated centers), weather effects should be reduced as far as possible. Only data taken under the following conditions were considered:
temperature from 25 to 28 °C,
relative humidity from 80 to 85%,
wind velocity (measured at 2 m height) 1.6 to 4.0 m s^{-1},
period of sampling 10.00 to 10.30 a.m.

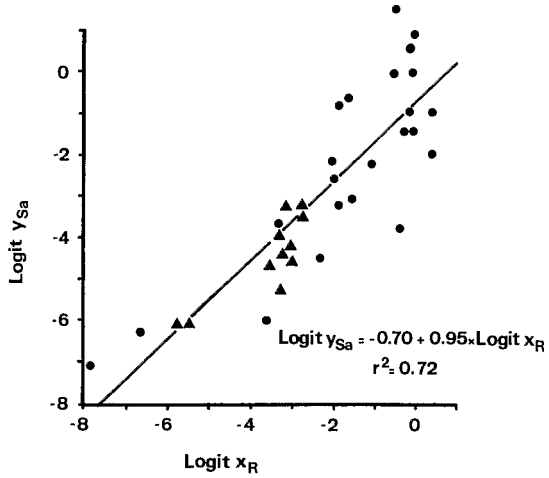

Fig. 1. Aerial dispersal of *Puccinia arachidis*. Spore content of the air (vertical axis) as related to rust intensity of the crop (horizontal axis).
x_R: relative pustule density, in number of pustules m^{-2} divided by the highest number found; y_{Sa}: relative spore content of the air, in spores m^{-3} divided by the highest spore content found; r: linear correlation coefficient; ▲: plot 1; •: plots 2, 3, and 4.

The choice of this sampling period was a compromise between the period of expected highest spore content, about noon (Mallaiah and Rao, 1982), and that of the lowest risk of rainfall, early morning.

Fig. 1 shows the selected data from the four plots (34 samplings). As a general trend, the spore content of the air (expressed as the logit of the relative spore density) increased with rust intensity (expressed as the logit of the relative number of lesions m^{-2}, X_R). Linear regression performed on these 34 sampling leads to the equation: logit $(Y_{Sa}) = -0.70 + 0.95$ logit $(X_R$ ($r^2 = 0.72$, with $r^2(0.99) = 0.15$). The regression is significant ($P < 0.01$).

Variation in the spore content of the air (plot 1). The results (Fig. 2) represent a relatively dry period, as no rainfall of importance occurred until the morning of the 5th day of the observation period. The spore content of the air (Fig. 2 A) shows a clear periodicity, peaking at about noon. Spore densities were highest when temperature and wind velocity were high and relative humidity was low. A relatively cool and humid morning, as on the first day, may have caused a delay of 2 to 3 hours in the appearance of the daily peak. Figures under the peaks are the total daily values, integrated over 24 hours beginning at 5.00 a.m. They do not show a general trend. Fig. 3 shows the diurnal rythm, determined according to Hirst (1953), under the prevailing dry weather conditions (drawn line). This curve conforms to those of Mallaiah and Rao (1982) (broken lines).

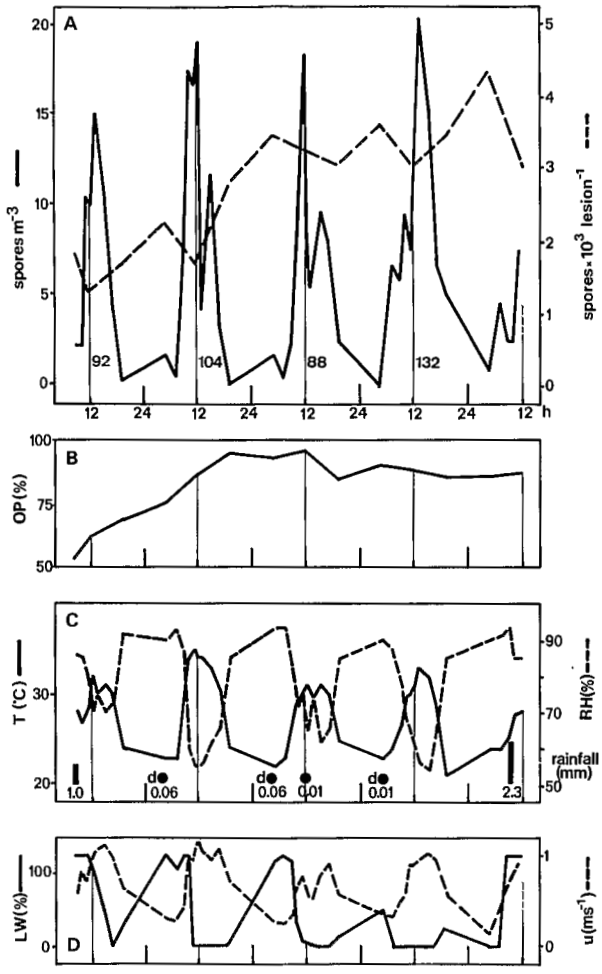

Fig. 2. Aerial dispersal of *Puccinia arachidis*. Diurnal periodicity of rust and weather variables in plot 1. Time is expressed in hours (horizontal axes).
A: Spore content of the air (drawn line, spores m^{-3}) and spore content of lesions (broken line, spores $lesion^{-1}$); B: Open pustules in percent (OP in %); C: Temperature (T in °C, drawn line), relative humidity (RH in %, broken line), rainfall (in mm, bars), and occurrence of dew (dots); D: Leaf wetness in percent of wet leaves (LW in %, drawn line) and wind velocity (u in m s^{-1}, broken line).

Variation of the spore content of lesions (plot 1). The number of spores per lesion (Fig. 2 A) increased during the observation period. The significant trend ($r^2 = 0.81$, $P < 0.01$) between the number of spores per pustule and time was superimposed over daily variations which were inversely related to those of the spore density in the air. The increase in the proportion of open pustules (Fig. 2 B) at the beginning of the experiment represents the sporulation wave following inoculation, and the increase in the number of spores per lesion represents the ripening of the pustules (Mehta and Zadoks, 1970).

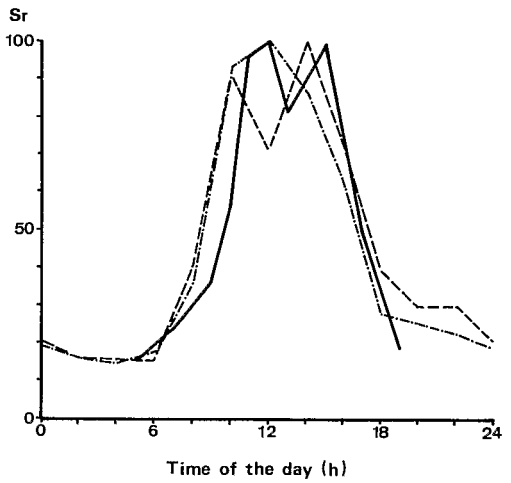

Fig. 3. Aerial dispersal of *Puccinia arachidis.* Diurnal periodicity of the urediniospore count of the air. S_r represents the observed spore density relative to weighted mean peak value, in percent. —— Plot 1 (see text): weighted means of four days representing dry weather conditions; ------ Mallaiah and Rao (1982): variation in one rainy season; · — · — · — · Mallaiah and Rao (1982): mean values for three cropping seasons.

Variation of the spore content of the air and of the spore content of lesions: regression analysis (plot 1). The variation of the spore content of the air (Sa) and of the spore content of the lesions (Sl) can be submitted to a regression analysis, introducing temperature (T), relative humidity (RH), wind velocity (u) and leaf wetness (LW) as explanatory variables.

Among the correlation coefficients listed in Table 1, those relating Sa to T and RH are high, while RH and T are strongly correlated. Since RH includes a direct effect

Table 1. Aerial dispersal of *Puccinia arachidis.* Linear correlation coefficients of rust and weather variables.

	Sa	T	RH	u	LW	Sl
Sa	1	0.75**	−0.75**	0.57**	−0.35**	−0.27
T		1	−0.89**	0.73**	−0.32**	−0.47**
RH			1	−0.72**	0.57**	0.26
u				1	0.28	−0.51**
LW					1	0.20
Sl						1

Sa) Spore density in the air (spores m^{-3}); T) Temperature (°C); RH) Relative humidity (%); u) Wind velocity (m s^{-1}); LW) Leaf wetness (%); Sl) Number of spores per lesion.
The correlation coefficients followed by * or ** are significant at $P < 0.05$ and $P < 0.01$, respectively ($r_{0.95} = 0.30$, $r_{0.99} = 0.39$).

Table 2. Aerial dispersal of *Puccinia arachidis*. Trend analysis: regression of the lesion content on time, and of the corrected lesion content on aerial spore density.

Explanatory variables											
general trend : t						daily variation : Sa					
variable to be explained	equation	r^2	reg.SS (df=1)	res.SS (df=41)	F (1.41)	variable to be explained	equation	r^2	reg.SS (df=1)	res.SS (df=41)	F (1.41)
S_l	$\hat{S}_l = 1582 + 25 \times t$	0.80	23.4×10^6	5.7×10^6	168**	$Sl - \hat{Sl}$	$Sl - \hat{Sl} = 219 - 31 \times Sa$	0.23	5.7×10^6	4.3×10^6	54.3**

t : elapsed time, in hours from the beginning of the experiment.
r : correlation coefficient.
Sa : spore content of the air (spores m^{-3}).
Sl : spore content of lesion (spores $lesion^{-1}$).
$\hat{Sl}$: estimated spore content of lesion, according to the regression equation for the general trend.
reg. SS : regression sum of squares.
res. SS : residual sum of squares.
F : Fisher's variance ratio.
df : degrees of freedom of sum of squares.

Table 3. Aerial dispersal of *Puccinia arachidis*. Multiple regression analysis of the spore density of the air on weather parameters in plot 1.

Equation number	Variable to be explained	Explanatory variables	Equations1	Significance of the regression		
				regression SS	residual SS	F
1	Sa	RH, u, S_l	Sa = 31.7 − 0.32 RH** + 0.62 u** − 3.9 10±4 Sl**	1166.8	599.7	19.0**
2		Δt = 1h	Sa(t) = 31.4 − 0.32 RH** + 0.02 Sa(t − 1)	750.0	630.3	23.2**
3		Δt = 2h	Sa(t) = 38.7 − 0.39 RH** − 0.25 Sa(t − 2)	785.5	540.3	27.6**
4	Sa(t)	RH, Δt = 3h, Sa(t − Δt)	Sa(t) = 41.5 − 0.42 RH** − 0.45 Sa(t − 3)**	886.8	437.4	37.5**
5		Δt = 5h	Sa(t) = 33.6 − 0.34 RH** − 0.19 Sa(t − 4)	757.6	491.4	27.0**
6		Δt = 10h	Sa(t) = 31.7 − 0.32 RH** − 0.30 Sa(t − 5)	740.2	740.2	25.3**

1 Significance of the contribution of explanatory variables in equations was tested with Fisher's F test (*;**: contribution significant at $P < 0.05$ and $P < 0.01$, respectively).
Regression SS : regression sum of squares, Residual SS : Residual sum of squares, Sa (t − Δt) : previous aerial spore density, Δt before the current (Sa(t)) spore density (missing data were estimated by linear interpolation).
For other symbol explanation, see Table 1.

of T, the latter variable is not considered in further calculations. The remaining variables with a high explanatory value for Sa are RH and u. Initially, no significant linear relation was found between Sa and Sl. If, however the variation of Sl was submitted to a trend analysis (Table 2), after correction for variation with time, it led to a significant relation with Sa.

In Table 3, equation 1 provides a summary of the relations between the variables which can be deduced from Fig. 2: RH and Sl are negatively correlated to Sa, while u is positively correlated to Sa.

The effect of time (t) on Sa is shown in equations 2 to 6, where the spore density, measured during a previous time interval (Sa ($t - \Delta t$)), is used as an explanatory variable of the next Sa value (Sa (t)). In regression 4 ($\Delta t = 3$ hours) this explanatory variable has a significant negative coefficient, suggesting that previous spore take-off interferes with subsequent spore liberation, due to the daily rhythm in depletion and repletion of uredinia.

Discussion

The variation in the spore content of the air during the first experiment (plot 1) ranged from 0 to 20 spores m^{-3}. This range is low in comparison to the data provided by the litterature on rust dispersal (Gregory, 1961; Ingold, 1971), and more specifically on groundnut rust dispersal (Mallaiah and Rao, 1982). In the latter case, values frequently reached several hundreds of spores m^{-3}. Similar values, up to 800 spores m^{-3}, were obtained from samplings performed at variable disease severity (plots 1, 2, 3 and 4) throughout the whole epidemic (Fig. 1). A significant, positive correlation was found between the spore content of the air and the rust intensity in the four infected plots, all under comparable weather conditions. The observations from plot 1 were taken at the beginning of the focus development, as demonstrated by the increasing proportion of open pustules (Fig. 2, B).

The comparison of Fig. 1 to the figures shown by Burleigh et al. (1969) for *P. graminis* and *P. recondita,* as well as the comparison of the coefficients of determination shows that in the case of groundnut rust the severity of disease has a lower explanatory value for the spore content of the air than in the case of the cereal rusts. This can be related, in part, to the use in this study of momentaneous spore counts instead of cumulative spore counts. Further analysis of such experiments should allow to estimate the explanatory value of other variables than disease intensity. Nevertheless, the result of this case-study supports the general validity of the method described by Burleigh et al.

P. arachidis shows a marked periodicity of the variables representing the state of the pathogen population (Fig. 2, A) in response to daily changes of weather parameters. Periodicity is a prevailing feature of fungal parasites of aerial plants parts, including rusts (Hirst, 1953). The periodicity presented here is in agreement with that of Mallaiah and Rao (1982).

The correlation matrix of Table 1 shows that many of the explanatory variables are intercorrelated. According to Butt and Royle (1974), this should not diminish the predictive value of the regression models which can be built from these data.

The equations in Table 2 stress the importance of some variables for the spore con-

tent of the air; among them, the effect of relative humidity (and /or temperature) is predominant. While Smith (1966) for *P. graminis*, and Rapilly et al. (1970) for *P. striiformis* demonstrated the importance of wind velocity, its effect on the spore content of the air is moderate in this analysis. It should be noticed that wind hardly varied during the observation period (plot 1 : 0 to 1.2 m s^{-1}, at canopy level), reducing its explanatory value in this set of data. Equations 2 to 6 of Table 2 introduce the previous spore content of the air at variable time intervals as explanatory variable of the current spore content. The significant ($P < 0.01$, Table 2) contribution of this new variable at the optimal delay of $\Delta t = 3$ hours indicates that the amount of spores in the pustules readily available for take-off is limited.

The multiple regression analysis of the data from plot 1 leads, as a main result, to a hierarchy of the weather factors affecting spore content of the air for the – relatively dry and calm – weather conditions prevailing during this experiment. Relative humidity is responsible for most of the variation and wind velocity ranks second as an explanatory variable. Further studies would be necessary to measure the effects of the weather factors considered here on the several subprocesses (Hirst, 1961; Smith, 1966 and Zadoks and Schein, 1979) leading to spore take-off and dispersal. The importance of short-term 'memory effects' such as those due to the limited amount of available spores in the pustule might then be revealed.

Two types of variation in spore content of the air above a groundnut canopy infected by rust were found in this study. The first, with a small amplitude (0-20 spores m^{-3}), observed at low levels of rust (plot 1), is related to daily changes in weather conditions; it represents daily rhythmicity. The second, with a large amplitude (0-800 spores m^{-3}), represents the epidemic trend. The hypothesis is forwarded that the daily rhythmicity in the spore content of the air can be extrapolated to the whole range of rust severities encountered during epidemics.

Acknowledgements

I am grateful to Professor J.C. Zadoks (Agricultural University, Wageningen, the Netherlands) for detailed analysis of this work and linguistic assistance. Thanks are due to Mr H. Voortman for assistance in field samplings.

Samenvatting

Relatieve luchtvochtigheid en windsnelheid en het dagelijks ritme in de verspreiding van urediniosporen van Puccinia arachidis

Vier veldjes met aardnoten in Adiopodoumé (Ivoorkust) werden in het groeiseizoen kunstmatig besmet met *Puccinia arachidis*. Gedurende het verloop van de daaropvolgende epidemie werd de mate van aantasting door roest bepaald en werden de gevangen sporen geteld. De sporendichtheid op gewashoogte varieerde van 0-800 sporen m^{-3}. Een significante lineaire regressie tussen de sporendichtheid en de roestaantasting (uitgedrukt in het aantal lesies m^{-2}) kon worden vastgesteld na logit transformaties van de relatieve aantallen. Gedurende de eerste sporulatiegolf na de inoculatie werden de sporedichtheid in de lucht en de hoeveelheid sporen in de sporenhoopjes periodiek bepaald. De hoeveelheid sporen in de lucht varieerde van 0

tot 20 sporen m^{-3}. Er werd een duidelijke dagelijkse ritmiek van de sporendichtheid in de lucht gevonden. Deze hield verband met het dagelijks ritme in het verlies en de aanwas van sporen in de sporenhoopjes. De belangrijkste verklarende factor was de relatieve luchtvochtigheid, gevolgd door de windsnelheid. Er wordt verondersteld dat de gevonden periodiciteit geldt voor de gehele variatiebreedte aan sporendichtheid, bepaald bij verschillende niveaus van roestaantasting.

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Book review

R.K.S. Wood & G.J. Jellis (Editors), 1984. Plant diseases: infection, damage and loss. Blackwell Scientific Publications, Oxford. 327 pp. Price £ 25.

'By the year 2000, ... world food production will probably need to increase by about 40%. Between 1950 and 1969, world agricultural production increased 1.7 times..., slightly more rapidly than world population (1.5 times). In the 1970s, the two are no more than keeping pace with each other'. These sentences, quoted from the introductory chapter of section 4 of this book, indicate the important tasks for plant pathologists. Better control of diseases and pests is necessary to increase food production. And to obtain better control, a good understanding of the biology of the agents that cause damage is essential, as are the reactions of the host plants when they become diseased. On this topic, the British Society for Plant Pathology held a symposium in December 1982, with participants from various parts of the world. This book contains the proceedings of the symposium.

The first section of the book deals with factors causing disease, such as toxins, cell wall-degrading enzymes and growth regulators. Whether toxins are determinants of pathogenicity is briefly discussed and examples are given on the involvement of cell wall-degrading enzymes in pathogenicity, as well as on the role of growth regulators in plant disease. Together, these chapters present a very good introduction to the theme of the book.

The second section deals with physiological responses of plants to pathogens, with information on effects on photosynthesis, respiration, transport systems, root functioning and tolerance (endurance) to parasitic infection. This part discusses experimental data that are not always considered by plant pathologists. For example, in Chapter 6, experimental data are discussed related to respiration of plant tissue infected by biotrophic fungi. These data indicate that enhanced oxygen uptake results from increased biosynthesis by which the host supplies the fungus with nutrients, rather than being part of the pathogenesis. There is strong evidence that incompatibility is associated with intense energy-dependent metabolic activities and with increases in the rate of respiration of the plant. It is, however, questionable, whether saprophytic micro-organisms lead to energy-requiring and thus to yield-reducing physiological reactions. I believe that the information, given in these chapters could be "eye openers" for plant pathologists, and not only for those working in the field of disease control.

The third section of the book gives information on infection and host damage. It includes an introductory chapter and examples from a wide variety of diseases: foot and root pathogens, foliar pathogens, bloom infections, vascular pathogens, gall development and host damage caused by viruses.

The fourth section of the book deals with damage and loss, the main topic of the symposium. After a good overview on world crop losses, several diseases are described as examples to demonstrate how damage can occur and how this can be prevented. It is interesting to note, that the data given by Cramer (Cramer, H.H., 1967. Pflanzenschutz-Nachrichten Bayer, Leverkussen) still form the basis for estimates of loss from diseases, pests and weeds. But new information is given, e.g. on market losses of fresh produce and on the economics of fungal control for cereal diseases.

Because of the purpose of the symposium, with 26 different aspects treated, the chapters had to be rather short. Some of them present a broad overview, others give more detail: the majority are well written and easy to read. Specialists may find the book superficial, especially since no attempt has been made to integrate the information. However I find the information presented and combined into one book highly relevant to plant pathologists, especially for those not directly working in the field of damage and loss. The book is well worth reading and should get a place in all libraries of agronomy and plant pathology. The price will be somewhat prohibitive for students to obtain their own copy, but it should be recommended for them to read it; some basic knowledge of plant pathology is essential to understand what is written.

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